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## Physiological Studies on Salt Tolerance of Crop Plants XV. Influence of Sodium Sulfate on Chemical Composition of *Cicer Arietinum* Seedlings

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Salinity considerations are likely to be an important feature of irrigation agriculture wherever it is practiced. The fact that depressed growth of many plants results from even moderate accumulation of sodium sulfate has practical significance. Furthermore, it is important that the mechanism of salt injury be as clearly understood as present day insight into the biological process will permit. Investigations at the U. S. Regional Salinity Laboratory, and elsewhere, have presented two choices in explanation of the injury mechanism, i.e., the osmotic or the toxic.

Observations on several species of crop plants indicating toxicity of high concentration of sulfate ions has been reported for flax (1), tomato (2), cotton and orchard grass (3), and leek (4). The toxicity has been attributed to an accumulation of the ions resulting in disturbed ionic uptake and ion accumulation (5-7). In these studies the investigations have invariably been conducted with photosynthesizing green plants grown in culture solution and the data does not satisfactorily correlate ion accumulation and growth response.

In the present investigation, therefore, an attempt has been made to understand the disturbance of the ionic balance in etiolated seedlings caused by growth in sodium sulfate solution. The experimental period was limited to four days of growth after sowing and quantitative changes in inorganic elements, nitrogen and sugar were observed. A toxic concentration (8) of sodium sulfate was used in the test experiments.

### MATERIALS AND METHODS

Gram (*Cicer arietinum* L.) seeds (N. P. 58) were surface sterilized and grown on moist filter paper in petri dishes at 28°C in a humid dark chamber during 96 hours. The control and treated sets received distilled water and 0.6% sodium sulfate solution respectively and

representative samples were collected from each at intervals of 48 and 96 hours. The seedlings were washed with distilled water and dried in a steam oven. Seeds were also dried and all samples were ground and preserved in glass-stoppered bottles for chemical and ash analysis. For the determination of protein nitrogen, in seedlings, similarly grown fresh seedlings were used.

The samples were digested (9) and the procedure for analysis of the inorganic elements as well as total nitrogen, reducing sugars and invert sugars were accomplished by established methods (10), using a Spectronic-20 photoelectric colorimeter. Protein nitrogen of fresh seedlings was determined by the Haskins modification (11) of the Koch and McMeekin technique (12) and protein nitrogen of the seeds was determined by biuret reaction (10). Analyses were conducted in triplicate and mean values are reported.

### RESULTS

The absolute values for the analyses are given in table 1. The progressive changes from seeds to seedlings, at each interval, are expressed as percent of the value of the seeds in figure 1, and for an understanding of the salt effect, the values expressed as percent of the respective controls are presented in figure 2.

The following data present details of the graphic data of figures 1 and 2.

*Potassium.*—The potassium content diminished slightly, the loss being 3.3% at the first interval and further loss of 1.1% was observed at the second interval in control seedlings. Reductions of 10.9% and 2.2% respectively, were found to occur in the test seedlings.

*Sodium.*—The concentration of sodium decreased 59.1% in control seedlings at the first growth interval but at 96 hours the concentration was 11.5% less than that in the seeds. In the salt-test seedlings the reduction was 14.8% and at 96 hours the concentration exceeded the seed content by 54.0%.

The K/Na ratio was markedly greater for control seedlings at the first interval, when compared to the ratio for seeds, while the ratio was lowest at 96 hours in the salt-test seedlings.

*Calcium.*—The amount of calcium in the seedlings was reduced and the decrease was greater at the earlier interval in both the control and salt-test seedlings; the magnitude of reduction was greater in the salt-test seedlings.

*Magnesium.*—The loss of this element at the first interval was exhibited in both control and salt-test seedlings and both groups recovered at the 96 hour interval.

### EXPLANATION OF FIGURE 1

FIG. 1. Influence of sodium sulfate on progressive changes in mineral composition, nitrogen and sugar (per cent of seed value). I potassium; II sodium; III calcium; IV magnesium; V iron; VI phosphorous; VII sulfate; VIII total ash; IX total nitrogen; X reducing sugars; XI invert sugars.

○ Seedlings grown in distilled water

● Seedlings grown in 0.6% sodium sulfate solution



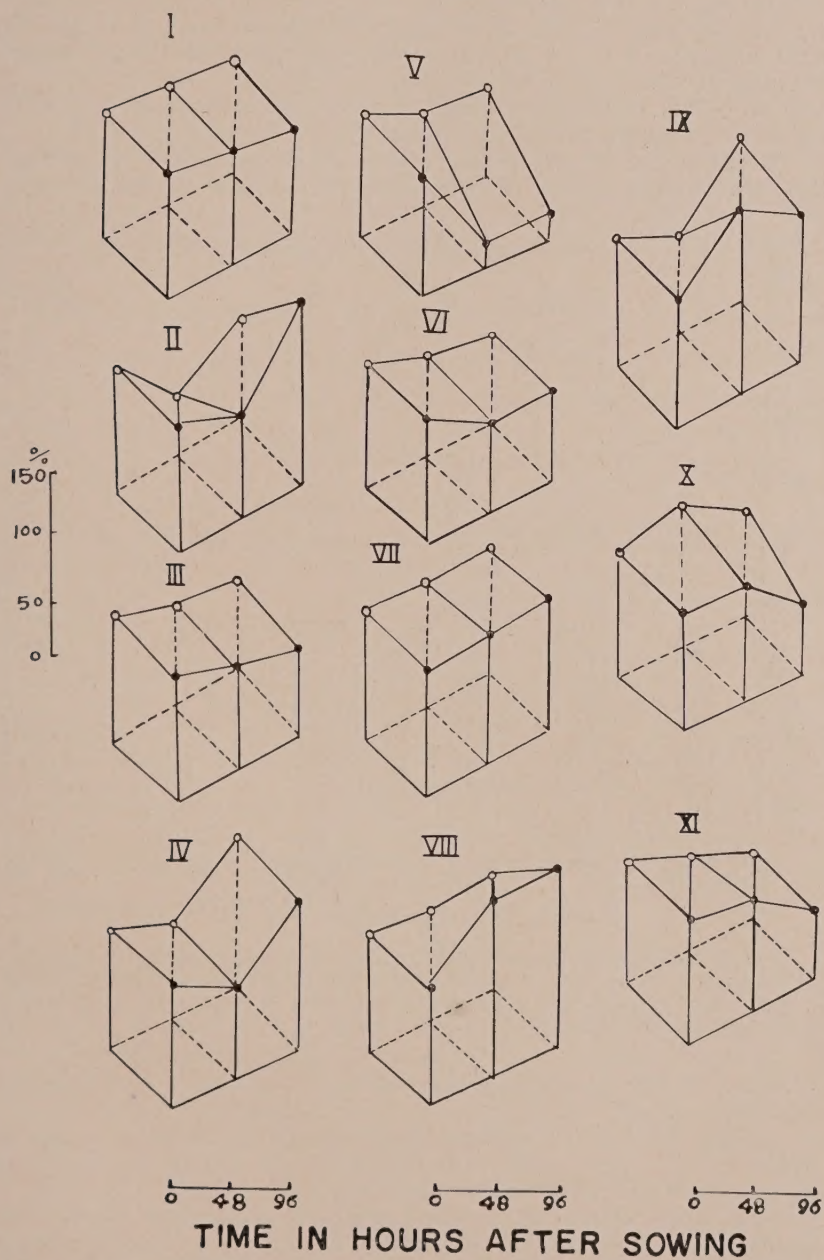


Figure 1

The Mg/Ca ratio remained equal to that of the seeds at 48 hours but was increased 66.6% at 96 hours. In the salt-test seedlings the ratio decreased, 8.4% at 48 hours and at 96 hours the ratio exceeded the ratio for seeds by 58.5%.

*Iron.*—The decrease at 48 hours in both sets was recovered only in the control seedlings at the second interval.

*Phosphorous.*—In the control seedlings the phosphorous content was reduced 20% at 48 hours and was further reduced, 8%, at 96 hours.

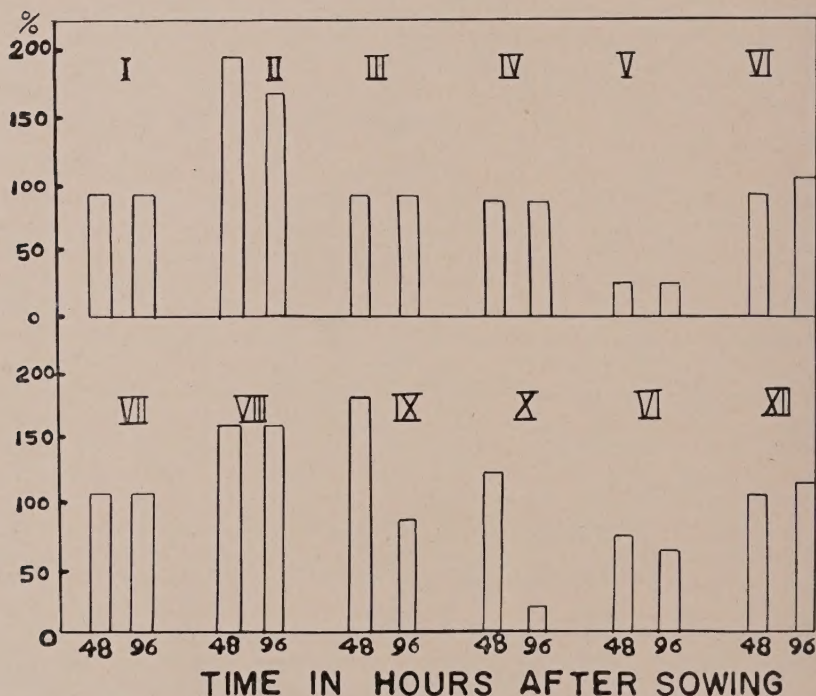


FIG. 2. Influence of sodium sulfate solution on mineral content, nitrogen and sugar (per cent of controls). I potassium; II sodium; III calcium; IV magnesium; V iron; VI phosphorous; VII sulfate; VIII total ash; IX total nitrogen; X protein nitrogen; XI reducing sugars; XII invert sugars.

In the salt-test seedlings a 24% decrease at 48 hours remained unchanged.

*Sulfate.*—The sulfate content remained constant in control seedlings and the amount gradually increased during the test period in sulfate supplied seedlings.

*Total ash.*—The total ash content of control seedlings at the first interval was 10.9% lower than that of the seeds and a further slight decrease was noted at 96 hours. In salt-test seedlings the total ash increased 48.5% at 48 hours and remained constant at 96 hours.

*Total nitrogen.*—In the control seedlings total nitrogen was lower,



18.9%, at 48 hours but at 96 hours the seedling content. In the salt-test seedlings the nitrogen was 50% greater at 48 hours and 20% greater at 96 hours than that of the seeds.

*Protein nitrogen.*—Protein nitrogen content was reduced during the growth period in both control and salt-test seedlings.

*Reducing sugars.*—Although a slight increase in reducing sugar content was noted in control plants at 48 hours, both sets of seedlings showed a loss at 96 hours; the greater loss occurred in salt-test seedlings.

*Invert sugars.*—Invert sugar content decreased 17.3% at 48 hours and 45.7% at 96 hours in control seedlings. In salt-tests seedlings the decrease was 8.7% and 37.1% respectively.

TABLE 1.—Effect of supplying sodium sulphate solution on mineral content, nitrogen and sugar (per cent dry weight).

	Seeds	Time in hours after sowing			
		48 hours		96 hours	
		Control	Na <sub>2</sub> SO <sub>4</sub>	Control	Na <sub>2</sub> SO <sub>4</sub>
Potassium.....	0.920	0.890	0.820	0.880	0.800
Sodium.....	0.061	0.025	0.052	0.054	0.094
Calcium.....	0.190	0.163	0.158	0.154	0.149
Magnesium.....	0.240	0.196	0.182	0.310	0.290
Iron.....	0.009	0.001	0.002	0.007	0.002
Phosphorous.....	0.250	0.200	0.190	0.180	0.190
Sulphate.....	0.033	0.033	0.034	0.033	0.036
Total ash.....	3.140	2.800	4.540	2.760	4.520
Total nitrogen.....	3.450	2.800	5.200	4.750	4.150
Protein nitrogen.....	1.920	1.080 <sup>1</sup>	1.320 <sup>1</sup>	0.560 <sup>1</sup>	0.120 <sup>1</sup>
Reducing sugars.....	0.170	0.190	0.160	0.150	0.100
Invert sugars.....	0.810	0.670	0.740	0.440	0.510

<sup>1</sup>Expressed as per cent fresh weight.

#### DISCUSSION

In this study, which sought to determine certain effects of sodium sulfate on Gram seedlings, the complexities associated with carbon assimilation were avoided and the experimental period was reduced to four days of seedling growth. All mineral constituents decreased as the seeds sprouted and grew in distilled water; potassium and sulfate concentrations were least affected. Seeds grown in sodium sulfate solution presented similar changes in mineral content but the magnitude of change was greater and sodium and sulfate ions accumulated in the seedlings.

Protein nitrogen and invert sugar content was reduced in both control and test sets during the total growth period while reducing sugars increased only in control seedlings after 48 hours and otherwise declined in all experiments. Total nitrogen content was reduced in both control and salt-tests seedlings at 48 hours but increased in each at 96 hours.

The alteration in accumulation of inorganic ions in seedlings supplied with a toxic amount of sodium sulfate occurring either as an increase or decrease compared to control plants, indicates a disturbance in the ionic balance within the cell. The present findings indicating a loss of potassium in plants grown in sodium sulfate solution support certain published reports (5, 6, 13) and are in opposition to reports by other investigators (3, 7, 14). A reduction in potassium has been shown (14) to bring about disturbances in the quantities of other cations and the phenomenon of lowered calcium associated with sulfate injury is reported (15) to condition cationic intake. In Gram seedlings the leaching of calcium is more pronounced in plants grown in sodium sulfate solution.

In the present study, the phosphorous content remained unaffected by the salt. Magnesium was reduced and ash content was increased in seedlings grown in sodium sulfate.

Disturbances were also observed in nitrogen and sugar contents of sodium sulfate-grown seedlings. Although total nitrogen increased and then decreased during the test period, protein nitrogen content was markedly reduced but remained higher than in control plants, and reducing sugar content was lowered during the test period but invert sugars remained higher than in control plants.

#### SUMMARY

The influence of sodium sulfate solution (0.6%) on the mineral composition, nitrogen and sugar content of dark-grown Gram (*Cicer arietinum* L.) seedlings have been reported. Seedlings were analyzed at 48 hours and 96 hours after sowing and the content of K, Na, Ca, Mg, Fe, P, SO<sub>4</sub>, total ash, total nitrogen, protein nitrogen, reducing sugars and invert sugars of test and control plants are reported.

All the mineral constituents except potassium and sulfate of seedlings grown in distilled water were partially leached. The seedlings grown in sodium sulfate solution exhibited a reduction in potassium and iron and only slight changes in calcium, magnesium, and phosphorous content. Sodium and sulfate increased in the test plants.

Total nitrogen of control seedlings was reduced and then increased during the test period while in test plants it rose above the seed level and then declined. The reducing sugar content rose above the seed level in control plants and then declined while in test plants the loss was continual during the test periods. Protein nitrogen and invert sugar loss was exhibited in both test and control plants.

These findings support previous reports and conclusions that the mechanism of salt injury is not identical among different species and the salt effect on the cell components individually or collectively probably represents an associated effect.

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## Early Evolution of Flower Types<sup>1</sup>

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In several previous papers the main problems of floral evolution have been discussed with regard to prevalent tendencies and observable trends in the differentiation of present-day flower types (35, 38, 40-45). It appeared appropriate to subdivide the whole floral history into six successive periods, each one represented by a corresponding evolutionary level and morphological "type class" among present-day flowers. These periods, levels, and classes, numbered I-VI, are shown in table 1.

The historical sequence of floral evolution is described in detail and pictured in a previous report (41, p. 471-473, fig. 2). According to a previous theory (38, p. 452) this sequence also mirrors the assumable sensory development of anthophilous insects, particularly their continuously increasing ability-grades to distinguish flower types.

Since flowers and insects are mutually interrelated in evolution as reciprocal selective factors, their historical development must necessarily concur in main points and periods. Consequently the sensory development of the anthophilous insects may be provisionally divided into six successive stages, which correspond to the above mentioned sequence of floral evolution. Actually these stages can be demonstrated in the ability-grades of insects to distinguish main flower types. Such "intelligence tests" are performed with present-day insect groups and their relative ability-grades are tabulated elsewhere (39, 41, 43).

In these circumstances it appears desirable to correlate the above mentioned sequence of floral evolution with paleontological records and to determine the main periods of this sequence in terms of the geological time-table. Beyond its great importance for floral ecology, such paleanthic time-table would also reflect to a certain extent the obscure history of the sensory development of anthophilous insects. Some tentative steps in this direction already have been made in a previous paper (35, fig. 3).

Unfortunately, fossils of angiosperms overwhelmingly consist of sterile plant parts, such as stems, leaves, fruits, pieces of wood, etc., or belong to anemophilous plants, predominantly trees, which do not possess showy flowers. Delicate blossoms of entomophilous angio-

<sup>1</sup>Much of the paleontological material used in this study is deposited in the collections of the Osborn Botanical Laboratory at the Yale University (original material of G. R. Wieland), New York Botanical Garden, and in U. S. National Museum, Washington D. C. O. Tippo, T. Delevoryas, W. C. Steere, H. F. Becker, and S. Mamay helped the author with valuable advice and suggestions during this study.

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sperms occur very infrequently, and only under extraordinary conditions have left fossilized remnants for identification of their typological characteristics. There are, for instance, in the Baltic amber (fig. 1) of the Oligocene many adequately preserved flowers which enable us to identify their type, form, and symmetry, as described by Conwentz (16). Further floral remains, mostly calices and sepals, have been preserved in compact clays, silts, muds, and in very fine sands. Flowers of *Diospyros*, (Ebenaceae), *Porana* (Convolvulaceae), *Rosa* (Rosaceae), and others are described by numerous authors (Heer, Berry, Knowlton, Lesquereux, Ball, Newberry, and others) and will be discussed in another paper.

#### INDIRECT APPROACH TO THE PROBLEM

Because of these difficulties various indirect methods must be elaborated for such paleanthic studies. First, the constancy of definite flower type can be established for certain plant groups, the fossils of which are known from some geological stratum. For instance, for the

TABLE 1.—*Evolutionary levels and type classes in the floral differentiation of entomophilous angiosperms, arranged in the historical sequence of their development.*

Periods	Evolutionary levels	Type classes*	Characteristics
VI	Superior	Zygomorphic	Bilateral symmetry
V	Protected	Stereomorphic	Third dimension
IV	Numeroid	Pleomorphic	Figure numerals
III	Radiate	Actinomorphic	Radiate symmetry
II	Simple	Haplomorphic	Spherical or semispherical
I	Primitive	Amorphic	No definite form

\**Type class* is defined in some previous papers (40, 41, p. 467, footnote) as a group of flower types of the same evolutionary level with similar principal characteristics. So far those described are: *amorphic*, *haplomorphic*, *actinomorphic*, *pleomorphic*, *stereomorphic*, and *zygomorphic* type classes.

genus *Magnolia*, living or fossil, the same haplomorphic floral structure is characteristic, with only slight variations in color and size of different species. This amazing fact was established after reconstruction of a Cretaceous magnolia flower according to a fossil petal from the Dakota sandstone (see below).

Several fossilized *Magnolia* leaves (*Magnoliaphyllum*) in Cretaceous and Tertiary thus indicate the possibility of the existence of haplomorphic flower types in those geological periods. Similarly constant is the haplomorphic floral structure of *Nymphaea*, *Castalia*, *Nelumbo* and other members of the family of Nymphaeaceae, whose mega- and microfossils are well documented since the post-Early Cretaceous period. A number of nymphaeaceous pollen grains are described from the Jurassic rocks already, but Scott (60) and other recent workers strongly doubt the authenticity of identification of these samples. Perhaps more reliable is a recent finding of an angiospermous leaf by Kuhn (31) from the lower Jura (see below).

Ranunculaceae, on the contrary, show a great variety in their floral structure, extending from haplomorphous through zygomorphic type classes among recent genera. It is therefore quite uncertain to try to predict the existence of some flower types according to fossilized leaves, pollen or fruits of the numerous members of this family.

Still further opportunities lie in the correlated study of certain flower types and the sensory development of their specific pollinators. Using the above described six-level evolutionary scale, it is possible to determine the ability grades of recent insect groups and to establish according to fossilized remnants of these groups their distribution in definite geological strata. Definite insect fossils may indicate therefore the possible existence of certain flower types in their synchronous floras.

In many cases primitive insect groups have survived from distant geological ages and are adequately represented in present-day faunas. The sensory behavior of these insects, particularly their ability-grade

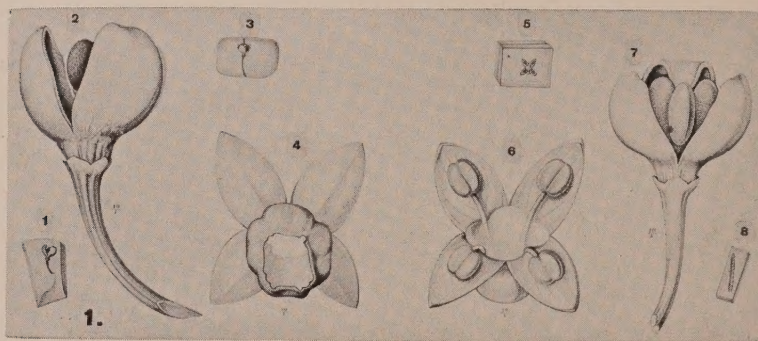


FIG. 1. Fossilized flowers from the Baltic amber (Oligocene), reproduced from Conwentz, 1886. 1-4, *Clethra berendtii* Casp. (Ericaceae); embedded in amber (1, 3); reconstructed (2-4). 5-7, *Myrsinopsis succinea* Conw. (Myrsinaceae); embedded in amber (5), reconstructions (6, 7). 8, *Andromeda imbricata* Conw., a branch in amber,  $\frac{2}{3}$  of natural size.

to distinguish flower types, can be studied and tested directly with the above described methods. Their anthophilous habits are commonly correlated with some sucking or chewing adjustments of their mouth parts, which anatomical structures can be traced back according to fossilized remains to their early existence and beginning of insect pollination.

#### ANTIQUITY OF MAGNOLIA FLOWERS

Many leading phylogenists, including Hallier (25, 26), Hutchinson (28, 29) and Wieland (66), consider Magnoliaceae to be one of the most primitive families of living angiosperms. Hutchinson (29, p. 421), for instance, regards *Magnolia pterocarpa* Roxb. from Himalaya "as being the most ancient living angiosperm, in fact like *Ginkgo*, almost a living fossil." Smith (62), on the contrary, believes that Winteraceae may be at least as primitive as magnolias. Bailey (3-5) and Canright (8-13), after a comprehensive morphological study, concluded that



closely related Degeneriaceae, Himmantandraceae, Magnoliaceae and Annonaceae, all hold primitive characteristics, at least in some of their reproductive or vegetative organs.

In this review we are interested mainly in the early flower types which might have attracted insects for pollination. In this regard, it is significant that all above mentioned primitive woody angiosperms bear haplomorphic flower types showing parallel trends of specialization within several families. In this group of primitive angiosperms, *Magnolia* provides us with the most important fossil evidence about the structure of a Cretaceous flower (see below). It is possible to reconstruct the full evolutionary sequence of a magnolia flower beginning with the Cretaceous period.

Close examination of a living magnolia flower reveals its apparent ancient features. Large white petals, numerous spirally disposed stamens, strobiloid arrangement of pistils, and perfect haplomorphic symmetry are the distinctive characteristics of the haplomorphic type class, which is second oldest in the above mentioned evolutionary sequence (see table 1). This means that the magnolia flower, in spite of its very long existence, has changed but little since its first known appearance in the Cretaceous period. According to paleobotanical records, the age of magnolias are roughly estimated to be 100 (19), and *Sassendorffites* about 175 million years old. Nevertheless the magnolia flower is still in the very beginning of the above mentioned evolutionary sequence (table 1), and very likely will remain in this archaic stage as long as the genus *Magnolia* exists.

This supposition is substantially supported by fossilized floral fragments found in the Cretaceous strata. There is a well preserved petal in the Dakota sandstone of Kansas, which in size, form and symmetry sufficiently resembles the petals of present day magnolias. After a close study of all the floral properties of this fossilized petal, it is not difficult to reconstruct the ancient flower of which this petal was a part. Its size, form, clearly recognizable petaloid venation, and haplomorphic symmetry leaves only little doubt about the construction and function of the early flowers of magnolias. Even the position of pistils in this ancient flower can be derived from the cone-like fruits, which have also, and more frequently than petals been preserved as fossils. For example, Reid and Chandler (51) have described 10 species of *Magnolia* of early Cenozoic age, exclusively according to fossilized fruits and seeds from the Eocene London Clay flora.

There can be little or no doubt that the Cretaceous magnolias were entomophilous and that the insect pollination must have been well advanced throughout the Mesozoic era. Similarly to magnolia, numerous Cretaceous species of *Liriodendron*, *Nymphaea*, *Nymphaeites*, *Castalia*, *Brasenia*, *Nelumbo*, and *Nelumbites* very likely possessed haplomorphic flowers, such as their present-day relatives still bear. From the material, available at present, it appears that the haplomorphic flowers were dominant in the Cretaceous period and that the amorphic type class has been already passed by early ancestors of angiosperms. However, many more flowering plants have been identified according to leaves and stems, which do not show any direct evidence to their floral structures.

Numerous entomophilous genera among Cretaceous plants indicate to a rich fauna of pollinators which must have existed already in that period and earlier. These pollinators must have reached to that time the second level in their sensory development and the ability grade to distinguish haplomorphic flower types. In regard to a very slow speed in the sensory evolution of insects, it is necessary to assume that the Mesozoic pollinators must have had a considerable experience with flowers during a long time, before they met with angiosperms. In these circumstances the below discussed view, that the early pollinators have worked with flowers of Bennettitales, seems reasonably justified.



FIG. 2-3. 2, A typical Triassic cycad (*Palaeocycas integra*) with megasporophyll (left), according to Florin. Notice the symmetrical arrangement of leaves around sporophylls on the top of stem. 3, A cauliflorous *Cycadeoidea dacotensis* according to Nathorst and Hirmer. Notice the difference between figure 2 and figure 3, dependent upon different arrangement of reproductive organs.

#### PALEOZOIC AND MESOZOIC FLOWER TYPES

Contrary to the general belief, our showy flowers, as we see them today, are not at all the sole products of recent flowering plants, but extend their origin far back beyond the age of angiosperms. There is some conclusive evidence and considerable paleontological proof that well-shaped flower types existed among some extinct groups of gymnosperms, a class which today contains predominantly wind-pollinated plants without showy blossoms. This is the order of Bennettitales in the class Gymnospermae.

It must be admitted, however, that the term "flower" hitherto has been used exclusively for indication of the reproductive organs of higher plants, particularly the showy blossoms of angiosperms or



"flowering plants." But there can be no doubt that the reproductive organs of Bennettitales are "true flowers" in the sense of euanthial angiosperms. Flowers of the Bennettitales contain sporophylls, semaphylls<sup>2</sup> and perianth, *i.e.* all essential parts, from which the complete flower of angiosperms is composed.

Sporophylls of the Bennettitales differ, however, from those of most ferns in being unlike the vegetative leaves of the same plant and in being restricted to certain reproductive branches. On the other hand the presence of well differentiated semaphylls, the distinctive characteristics of entomophily, conclusively points to the analogical function of the flowers of the Bennettitales and angiosperms.



FIG. 4-6. Reproductive organs (flowers) of the *Cycadeoidea dacotensis* according to Wieland, 1906, p. 165, 164, 110. 4, Unexpanded bisporangiate strobilus, with part of the enveloping bracts removed. 5, Longitudinal cut of the strobilus, with one frond folded (left) and one expanded (right). 6, A longitudinal section of ovulate strobilus.

Numerous petrified flowers of Bennettitales express not only perfect form and symmetry in their morphological structure, but also point to similar evolutionary sequence in their historical development as described above for the present-day flower types (fig. 7).

There is therefore good reason for the re-examination of the available floral residues of these ancient plants with the above described typological methods, in regard to the contemporary and ancient insect fauna. A novel paleo-hologenic approach is gradually crystallizing out of this study; a new method to deal with the evolutionary problems of ancient organisms from the standpoint of the organismic whole or holon (41, p. 469; 42). One practical value of this new approach is its

<sup>2</sup>Semaphylls are described in a previous paper (38) as "food marks" or "trophosemeions" of pollinators which guide visitors to their food plants. In contrast to "sporophylls" which are stamens and pistils of ordinary flowers, semaphylls are formed from petals, sepals, staminodia, bracts or colored upper leaves. Semaphylls and trophosemeions are different from "nectar guides", which are special pointers of nectar deposits inside of flowers.

adaptability for revaluation of existing fossil flowers and for reinterpretation of some previous conclusions.

Due to the highly creditable achievements of several prominent workers in the field of paleobotany, in particular the classical investigation of Wieland (66), we now know the flowers of the Bennettitales in detail. There is a striking analogy between the floral structures of these ancient gymnosperms and those of recent angiosperms. Both groups have the same essential flower parts, a central pistil (or pistils), surrounding whorl of stamens, and an enveloping perianth (see fig. 4, 5, 6). Some haplomorphic flowers of the Bennettitinae resemble those of primitive angiosperms, particularly those of *Magnolia*, *Liriodendron*, Nymphaeaceae, and Ranunculaceae (20, 58, 59, 66). Even some shades of colors are assumed for the ancient flowers of the Bennettitinae (20, 30, 59), possibly white and yellow (see below). But there are also some more generalized "paleomorphic" types among the Bennettitales which do not occur in the living angiosperms (fig. 7). Some further flowers are specialized in their own way and do not match any of the present-day flower types.

If we arrange all the known flower types of the Bennettitales according to their presumptive evolutionary sequence, three clearly distinguishable type classes, corresponding to three evolutionary levels, can be established: amorphic→haplomorphic→actinomorphic. Except the amorphic, all other types are represented also by the recent angiosperms, though they are molded in the latter case from entirely different material. These three type classes of the Bennettitales can be characterized briefly, as follows:

(I) *Amorphic* types (fig. 7: I) are molded from special floral elements, called semaphylls (38, table 2, p. 448, and definition p. 452), which differ structurally and functionally from the sporophylls of anemophilous plants. Their amorphic arrangement, however, does not give to the flower any special form or symmetry. Semaphylls serve as "food marks" (trophosemeions) for pollinators and for that reason have a special form and coloration. In higher plants they are formed frequently from colored bracts, perianth, petaloid stamens, colored spathes, anthodioid inflorescences, and deformed upper leaves. In all known flowers of Bennettitales, semaphylls were formed very likely from perianth, or from reduced sporophylls. In spite of this most heterogeneous material from which semaphylls are formed, in the Bennettitales and angiosperms, they all represent some definite sign or symbol of the above described floral system.

It should be noted here that the primary amorphic types are not known in recent flowering plants (38, p. 448). The lowest known angiosperms such as *Magnolia* and Nymphaeaceae possess flowers of haplomorphic type class. But secondarily developed amorphic types appear among angiosperms in various evolutionary levels, in particular when a wind-pollinated plant turns over to insect pollination. Such cases are quite common among the Compositae, Euphorbiaceae, *Dichromena*, etc. (36, 41).

(II). *Hapломorphic* types (fig. 7: II) represent simple flowers mostly with hemispheric arrangement of semaphylls and sporophylls, such as



flowers of *Magnolia* and water lily. Among Bennettitales haplomorphic types occur in *Cycadeoidea*, *Williamsonia*, *Wielandiella* and others.

(III). *Actinomorphic* flowers (fig. 7: III) are characterized by radial symmetry, while peripheral wreath-like semaphylls and central sporophylls occur on the same plane level. *Sturianthus* Kräusel (30) is a representative of the actinomorphic type among Bennettitales.

It is appropriate to mention here that a common tendency of the Bennettitalean flowers is to gather their stamens (microsporophylls) into a tubular assemblage, resembling somewhat the monadelphous androecium of *Malva* or the funnel form of *Convolvulus*. Such floral arrangement misled Wieland (67) who sought genetic affinities between the Mesozoic Cycadophyta and modern Malvaceae and Convolvulaceae. However, a more plausible explanation of this floral structure might be sought in the functional analogy rather than in the genetic homology of distant taxa.

(IV-VI). *Pleomorphic*, *Stereomorphic* and *Zygomorphic* types, common among higher flowering plants, are not known in the group of the Bennettitales. These types first appeared among angiosperms in the upper Cretaceous, expanded in the Tertiary, and are common in recent floras.

In current literature the stereomorphic and zygomorphic type classes are commonly traisted under various groups of sympetalous flowers. The animal-plant relationship of these flower types and their evolutionary adaptation to insect visitors are discussed by Wernham (65), Robertson (52-55), Betts (6), Sporne (63), Grant (21), and Leppik (35, 41-45).

#### ASSUMED FUNCTION OF THE FLOWERS OF THE BENNETTITALES

Wieland (66) seems to have been the first to recognize in the peculiar reproductive structures of the Bennettitales true flowers in the sense of angiosperm anthemia. Impressed by striking floral similarities in both groups, he attempted to derive angiosperms from the Bennettitales. This method was adapted by Arber and Parkin (1) as the factual basis for their "anthostrobilus" theory. These authors also emphasized the flower-like strobili of the Bennettitales and recognized the entomophilous character of the group together with the role of entomophily in the early evolution of angiosperms. Similar thoughts were expressed by Robertson (52-56) and Betts (6) about the mode of pollination of the primitive angiosperms.

Recent writers, Parkin (49), Scott (58), Seward (61), Gothan and Weyland (20), and Kräusel (30), among others, almost unanimously accept Wieland's interpretation, but they doubt the feasibility of deriving more advanced flowers of angiosperms directly from the Bennettitales. Microsporophylls of the latter group, for instance, have more resemblance to the fronds of ferns (*Marattia*) than to the stamens of angiosperms. The same difficulty arises in the case of some flower types among Bennettitales, which have united their stamens into a tube and show, according to Wieland, a remarkable affinity with higher Dicotyledoneous families, such as Convolvulaceae and Malvaceae. In spite of this superficial similarity, an impassable

gap remains between the Bennettitales and higher angiosperms in respect to their genetic relationship. After all, the floral similarity between these two groups rests upon the shape and symmetry rather than on the morphological homology, and need therefore not necessarily indicate the genetic relationship of these distant plant groups.

Wodehouse (68), studying the evolution of pollen grains, found that principally the same type was common to many primitive plant groups, such as Cordaitales, Cycadales, Bennettitales, and Ginkgoales. The pollen grains of *Magnolia* are scarcely distinguishable outwardly from those of the Bennettitales.










EVL. STAGE	FLORAL EVOLUTION OF			TYPE CLASSES
	CYCADEOIDEAE	WILLIAMSON.	ANGIOSPERMS	
III	 3.	 6.	 9.	ACTINO- MORPHIC
II	 2.	 5.	 8.	HAPLO- MORPHIC
I	 1.	 4.	 7.	AMOR- PHIC

FIG. 7. Comparative sketch of floral evolution in Cycadeoideae (A), Williamsoniae (B), and Angiospermae (C). Evolutionary stages I, II, III, (left) correspond to the type classes (right). 1, *Dioonitocarpidium pennaeforme* from Trias; notice the difference between semaphylls (sporophylls) and vegetative leaves, according to Kräusel, 1950. 2, *Cycadeoidea dactyloides*, according to Wieland. 3, The same in full bloom. 4, *Wielandiella angustifolia* from Rhaetia, Sweden according to Halle and Gothan (1954). 5, *Williamsonia spectabilis* and *W. whitbiensis*, both from Jura, according to Kräusel, 1950. 6, *Sturiantus langeri* from Trias, according to Kräusel, 1950. 7, Hypothetic amorphic type of angiosperms. 8, *Magnolia* type. 9, Diagrammatic sketch of an actinomorphic flower of angiosperms.

Scott (58, p. 96) raised the question about the function of the flowers of the Bennettitales, suspecting them in insect pollination. These flower-like strobili must have been striking objects when fully expanded, rivaling in size and modelling, the largest flowers of the present day entomophilous plants. But there are no indications in the paleontological records that insect pollination might have been established by the end of Paleozoic or in early Mesozoic eras. Thus the



function of these ancient flowers remained obscure to the early students of the Bennettitales, unless the whole problem could be approached from an entirely different angle.

In the light of present study, the problem now appears simple and basically solvable. The evolution of these early flowers shows a striking correlation with the normal sensory development of anthophilous insects, particularly when the floral form and symmetry are considered. Early cycads and the Bennettitales have left us abundantly well preserved floral fossils in which we can study their typological characteristics.

The perfect symmetry and regular form of paleozoic cycads (fig. 2) must have stimulated quite definitely the sensory development of food-searching insects until they were able to distinguish cycads from ferns, horsetails, lycopods, and other primitive herbs. The higher food value of the reproductive organs of cycads and Bennettitales very likely offered a particular chance to those insect groups, which were able to recognize cycads and select them out of the dominant mass of sporophytes.

In these circumstances the awakening of some elementary sense recognizing form and symmetry in contemporaneous flowers in more specialized insect groups would be a natural consequence of their food searching activity. But the possession of these important senses offered an undisputable advantage to their bearers in the natural struggle for existence.

Selecting flowers with definite typological characteristics for their permanent visits, these early insects unconsciously started to exchange pollen of different plants of the same species. As soon as this happened, the true insect pollination was established, and a new way was open for both, insect and plants, to move toward a unique evolutionary expansion in a way not known before that time among land organisms.

This important adaptation of early insects to their contemporaneous floral environment obviously took place by the end of the Paleozoic era and progressed further in the Mesozoic era. From that point on the early flowering plants were probably subjected to an intensive selection, carried on by food searching insects. In this mutually interrelated evolution every new sensory level in insects must have created a new type class among flowers. Once fixed genetically, this type remained constant for a long time, until some new gene combination and subsequent insect selection had given rise to the new trend. Step by step in this way the whole evolutionary sequence has been established, as pictured in fig. 8. The early history of this long lasting synagonism between insects and plants is distinguishably printed on the paleozoic rocks, and can be interpreted now with the above mentioned methods.

The first *amorphic* (paleomorphic) flower type appeared in the Permian age or possibly earlier, as pictured in fig. 7 (1). This most primitive "flower," although composed of ordinary sporophylls and bracts only, without particular form or symmetry, has been nevertheless clearly distinguishable from the flower clusters of anemophilous cycads. To make the flowers still more distinctive, a series of special

structures, semaphylls, were formed out of bracts or sporophylls. These were the early predecessors of petals and sepals of true flowers.

Several special trends and tendencies soon appeared in the evolution of these early flowers. One of the most remarkable achievements was undoubtedly the early development of cauline flowers on the stems of Cycadioideae. The separation of flowers from the vegetative leaves and transplacement of them on the stem (compare fig. 2 and 3), undoubtedly increased their visibility, not only for flying insects but also for crawling insects which lived on the earth. However, it is not yet known exactly which group of wingless insects were involved in plant pollination at that time. In any case the further development of these cauline flowers of the Cycadioideae followed the above described normal evolutionary sequence from amorphic to haplomorphic and actinomorphic levels, as pictured in figure 4-6 and figure 7, first column (A).

Contrary to the Cycadioideae, the flowers of the *Williamsonia* and *Wielandiella* developed on the long pedicels, making them inaccessible to crawling insects. But, even so, their general evolutionary trend remained the same, from amorphic through haplomorphic to actinomorphic (fig. 7, second, B column). In spite of several further specializations among the flowers of the Bennettitales, in their evolutionary sequence they all followed the general trend, which is further recapitulated also in the floral evolution of primitive angiosperms (see fig. 7, third, C column). Thus the same evolutionary sequence has been repeated in three different series of genetically unrelated plant groups independently of each other during three latest geological eras: Paleozoic, Mesozoic, Cenozoic. These series could be called therefore: Paleanthic, Mesanthic, and Cenanthic (see three columns, A, B, C in fig. 7).

#### SOME ANALOGIES BETWEEN THE FLORAL STRUCTURES OF BENNETTITALES AND COMPOSITAE

*Sturianthus* (*Sturiella*) *langeri* Kräusel has numerous small carpels (megasporophylls) concentrated on a flattened disk and surrounded by many ray-like male organs (fig. 7: 6). This unusual flower of a gymnospermous plant has been compared with the helianthoid capitulum of the Compositae, particularly with flower heads of the daisy and the sunflower (20, p. 310; 30, p. 85). Yet the capitulum of the Compositae is actually not a flower but a secondary structure, formed by compilation of numerous florets which are strictly stereomorphic. Consequently the flowers of *Sturianthus* and Compositae are not comparable either morphologically or phylogenetically since they belong to unrelated categories, such as gymnosperms and angiosperms. On the other hand, similar floral patterns may evolve in response to the selective activity of insects which have reached the same stage of sensory development.

Ample evidence exists that the differentiation of the capitulum of the Compositae is but a recapitulation of the process of floral evolution (44), including the main trends of the Bennettitean flowers. From this viewpoint the striking resemblance between floral patterns of the Bennettitales and of the angiosperms appears highly plausible, support-



ing the theory that entomophily must have been a decisive factor in the floral evolution of both groups. As a matter of fact, both these floral structures have the marked characteristics of beetle flowers, and beetles are known to have been the dominant insects throughout the Mesozoic age, as they still are the prevalent pollinators for recent Compositae.

Stebbins (64) has summarized the available evidence, both direct and indirect, of a possible Mesozoic origin of the Compositae. A series of structures described by Newberry (48) from the Upper Cretaceous Amboy clays of New Jersey resemble a "helianthoid flower with 20 or more ray florets" (48, p. 125). Stebbins (64, p. 657) and Cronquist (16a, p. 493) have compared Newberry's drawings with the capitula of living composites and found the fossils to have a sufficient resemblance to the tribe Heliantheae. But they disagree with Newberry's interpretation of fossilized ray florets, which Stebbins regards as "the persistent receptacular bracts or paleae of an involucre from which the flowers have withered and the achenes have fallen. In the modern species of *Wyethia*, and other genera of the tribe Heliantheae, these denuded involucre persist on the plant from one flowering season to the next, and are of such a tough, resistant character as to be admirably adapted for preservation."

But even so, the fossil structures from the Amboy clays have such a strong resemblance to the flowers of the Bennettitales that Newberry (48, p. 126) first labelled them as *Williamsonia*. It is regrettable that these fossils do not provide any evidence for the structure of individual flowers, which may or may not be true disc florets of the Compositae.

#### EARLY POLLINATORS

One crucial point for the present study is whether or not pollinating insects already existed in late Paleozoic and early Mesozoic eras, in the flourishing time of the Bennettitales. A further task is establishing the ability-grades of these ancient insects in recognizing their contemporary flower types. It is admittedly a curious problem, this attempt to comprehend psychic faculties of insects who lived hundreds of millions years ago and are actually known to us only from their petrified remains. There is no question but that some few decades ago such an attempt would have been condemned as worthless speculation, like any unintelligible causal or teleological interpretation of nature. But after the newly-made achievements in both fields, the sensory physiology of insects and floral ecology, such an approach to the problem appears pertinent now and methodically feasible. As a matter of fact, these early insects have left us in addition to their petrified remains, definite evidence of their sensory abilities and selective activities which enable us to comprehend their early way of life.

According to paleontological records, there were during the epoch of Bennettitales abundant insect groups which already had anthophilous characteristics (mouth parts) and belong now to the foremost pollinators of the present-day flowering plants (see table 2). Coleoptera (beetles) and Hemiptera (bugs) were first found in the Permian and became very abundant in the Triassic deposits. Hymenoptera (wasps)

appeared in Jurassic, Lepidoptera (butterflies, moths) in early Tertiary, or possibly already in the Cretaceous. Insects of the Tertiary period consist almost exclusively of families now living and to a large extent of living genera (14, 15, 27). Since many groups of these insects needed nectar, pollen, or at least plant juices for their existence, there seem to be no obstacles for the possible development of entomophily among Permian and Triassic Bennettitales.

It remains to be considered now to what extent these early insects, if they really were pollinators, could distinguish the rather advanced flower types, such as those exposed to them by the contemporary Bennettitales. Yet all the above mentioned insect groups are not only abundant in the present-day faunas, but also contained widely acting "professional" pollinators besides occasional "amateurs." It is important therefore to determine first the ability-grades of the present-day insects with the above described methods.

This writer tested recently several groups of "professional" pollinators, such as the honeybees (*Apis*), bumblebees (*Bombidae*), stingless wild bees (*Melaponidae*), some beetles (*Coleoptera*) and tropical butterflies (*Lepidoptera*) in respect to their ability to distinguish flower types. Using the above described yardstick of six ability-grades, the highest grade of every species could be determined in field tests. Except for some special cases, various species of the same group showed in these tests an astoundingly similar ability-grade, no matter where they lived. Beetles, for instance, remained in the beetle level, bumblebees on their level in the European and American continents from far north to the tropics. Results so far reported can be learned from the papers referred to at the end of this article (32-39, 43).

This study showed that all tested groups of recent insects are proficiently capable of distinguishing all such flower types as described for the Bennettitales, and beyond this many higher types which did not yet exist in the early Mesozoic era. And, as mentioned above, all tested groups, except *Lepidoptera*, were already well established in Permian and Triassic periods, at a time when Bennettitales were abundant. There is therefore little or no doubt that these insects were involved in pollination of contemporaneous flowers.

It remains to consider further the older groups of plant eaters, which occasionally act as pollinators.

Porsch (50) in an extensive study showed that many recent representatives of old insect groups, feeding on pollen, nectar, and soft flower parts, frequently act as carriers of pollen from one flower to another. More than a hundred species, representatives of thirty-two families and eleven orders, have been found involved in the process of pollination (table 2). Many of these insects, devouring or sucking plant leaves, may occasionally act as pollinators. Others are constant pollinators, looking for nectar and pollen only and visiting regularly definite flower types, as exemplified below.

*Taeniothrips ericae* (*Amblythrips*) Haliday is a small thrips of the order Thysanoptera, which feeds on nectar and uses urceolate flowers of *Erica tetralix* for shelter and as mating places and lays its eggs in the soft tissue of petals. According to Hagerup (23, 24) males of this thrips are rare and wingless, remaining for most of their life inside the



flowers. But the females are more active, flying from flower to flower in order to find males, and thereby becoming energetic pollinators. After mating, they lay eggs into the tissue of the soft corolla. Larvae remain inside their floral shelters where they feed on nectar and eventually leave the withering corolla with pollen loads on their backs. Such a highly specific way of life caused this thrips to adapt itself to a higher stereomorphic flower type, normally accessible only to higher pollinators. Porsch (50, p. 124) found even a still more primitive stonefly, *Chloroperla torrentium* Pict. of the order of Plecoptera, being adapted to *Listera ovata*, an orchid of the highest zygomorphic type class.

Reference may be also made to several other papers dealing with the problems of early pollination. Diels (18) believed that the earliest pollinators were beetles and that the primitive angiosperms were cantharophilous.<sup>3</sup> He indicated that during the rise and expansion

TABLE 2.—*The first occurrence of anthophilous insect orders in various geological strata.*

Geologic periods	Occasional pollinators	Steady pollinators
Tertiary.....		Lepidoptera
Cretaceous.....		
Jurassic.....	Trichoptera, Diptera	Hymenoptera
Triassic.....	Orthoptera	
Permian.....	{Thysanoptera	
	{Mecoptera, Plecoptera	Coleoptera
Carboniferous.....	{Neuroptera, Hemiptera	
Devonian.....	Apterogytia?	

of angiosperms near the end of the Mesozoic era, Coleoptera were abundant, and that the living flowering plants with primitive characteristics, such as *Magnolia*, *Nympheaceae*, *Eupomatia*, *Calycanthus*, and others are still pollinated by beetles. Grant (22) proved that a small beetle of the family Nitidulidae is responsible for pollination of the *Calycanthus occidentalis* Hook. in California and that the floral mechanism of this plant excludes most other insects. This author also considers beetle pollination to be the original condition in flowering plants.

A further correlation of morphologically primitive flowers with beetle pollination is seen by Brown (7) in the scarcity of nectaries in Magnoliaceae. He found nectaries only in *Magnolia coco* (Lour.) DC. and in *Talauma*. According to Daumann (17), *Calycanthus floridus* L., on the contrary, secretes a small amount of nectar from the tips of the inner staminodia. Beetles are knowingly not very specific to nectar, but eat pollen, ovaries and any soft flower parts.

In the case of Bennettitales, beetle pollination appears to be the

<sup>3</sup>*Cantharophilae*, a technical term for beetle flowers, introduced by Delpino (1870), but little used in current literature.

most acceptable supposition to many writers dealing with this problem. Diels (18) and Porsch (50), emphasizing the fact that some living cycads, including the genus *Encephalartos*, are pollinated by beetles, consider Bennettitales to be cantharophilous. Grant (22) supposes that beetles were the only important flower-visiting insects in existence during the Mesozoic era.

From this short review it is evident that the primitive Permian insects, as we know them according to their fossilized remains and from the anthophilous behavior of their living successors, *could not miss the early flowers of Bennettitales*. These facts indicate that insect pollination might have been established in the Permian and expanded in the Triassic period. Flower types of Bennettitales existing during this period have already been differentiated into several type classes.

#### THE SENSORY EVOLUTION OF EARLY POLLINATORS

In regard to the sensory evolution of pollinators, we must remember that the main change in insect fauna from the palaeopterous orders to the Neoptera and the general distribution of the latter group took place almost simultaneously with the expansion of Cycadophyta and Bennettitales in the Upper Carboniferous and Permian strata. The food-searching activity of these early plant eaters and later flower visitors in the midst of symmetrical cycad leaves and sporophylls of the Bennettitales must have been highly stimulating to their sensory development, in particular to their ability to distinguish objects of definite form and symmetry (fig. 2-7). However, it needs only a very short progressive step in the sensory development of insects to reach the ability-grade for discrimination of the first paleanthic flower type, and this progression very likely took place as a parallel development in several insect groups at the same time. Similar elementary mutualism still exists between some recent cycads and primitive insects and is described comprehensively by Porsch (50).

Exploitation of various food resources might have enabled insects to acquire surprising diversity and specialization as early as the Upper Carboniferous, with an increasing progress in their sensory evolution in Permian and Triassic periods. According to paleontological records the dominant insects of the late Permian were true bugs, or Homoptera, which were clearly adapted for feeding on plant juices (15, p. 266). Later on appeared beetles, or Coleoptera, the first representative of "professional" pollinators. Neither bugs nor beetles are known to surpass in their sensory development the radiate level of actinomorphic flower types. But even at this level they could have been able to distinguish all known flower types of their contemporaneous Bennettitales.

The Jurassic fauna is still characterized by insect groups whose ability-grades today do not reach much above the radial level. True flies, or Diptera, and the Hymenoptera were at that time almost exclusively parasitic types, very likely not yet conditioned to flowers. The aculeate insects, such as bees and wasps, were still absent (15, p. 267). Although primitive angiosperms might have appeared in Jurassic, they did not yet represent any new flower type, but recapitulated the existing types of the Bennettitales.

Nevertheless, these early pollinators with their higher mental capabilities opened a new era in the organismic evolution, preparing the ground for still higher forms of synagonism, which followed with the appearance of professional pollinators and higher angiosperms.

#### GENERAL CONCLUSIONS

Most paleontologists agree today that descending from some symphyla-like ancestors insects reached their wings in the lower Carboniferous and attained complete metamorphosis in the lower Permian strata (15). This means that these six-legged creatures, as we see them today, had completed their early evolution long before the appearance of birds, reptiles, and angiosperms, as well as higher animals and man.

These early insects presumably fed either on plant juices from the club mosses and tree ferns or were predators (15, p. 263). But they must have found out also the superior food qualities of the reproductive organs of flowering plants, as soon as these appeared on the scene.

In the light of present study it appears that insects during their later development in the Mesozoic and Cenozoic eras have undergone comparatively fewer changes than the plants upon which they fed. Anthophilous insects undoubtedly have progressed enormously in their sensory evolution and have modified also their mouth parts for nectar sucking purposes. But this is rather a steady and slowly proceeding change, scarcely comparable with the accelerated speed and countless special trends in floral evolution. This sensory evolution of anthophilous insects is reflected in the historical development of flower types, the latter being imprinted in the fossilized remains of early flowers.

There is considerable conclusive evidence and some paleontological proof that entomophily was already well established among Bennettitales in the Permian period. Otherwise these early gymnosperms would not and could not have developed showy bisexual and protandrous flowers, such as those produced only by entomophilous plants. Even more indicative is the fact that these early plants were able to produce semaphylls that can be co-ordinated into the same evolutionary sequence as that established for the flower types of higher plants.

Since the very beginning of anthophily, insects must have exercised strenuously in trying to locate their food plants according to some showy characteristics, such as color, odor, shape, size, etc. Such activity must necessarily have stimulated the further sensory development of pollinating insects, particularly their ability to distinguish contemporary flower types. Quite obviously plants with better arrangement of their showy parts could attract more qualified pollinators than the plants with less beautiful flowers. Better pollination must have favored seed production and more rapid spread of plants preferred by insects.

Yet the evolutionary progress of entomophilous plants depends mainly upon their genetic responses to the challenge of insects, realized in an increased production of new gene-combinations and visually distinguishable variations, necessary for the facilitation of the selective work of insects. Such preliminary conditions may arise when pollinators, for some reason or other, are continuously crossing certain varieties



or ecotypes among each other, as long as polymorphism appears within these plant groups. Further crossings and subsequent selections then may produce within these polymorphic species new types, which fit better to the insect needs, even though they may look quite different from the material from which they are molded. The proper conditions by which pollinators quit their common habit of type steadfastness and species constancy, and start to mix pollen of various types among one another, are well demonstrated among recent flowering plants as described elsewhere (13, 41). In this simple process of selection, the same insect groups, or different groups with similar behavior could initiate similar flower types in different places and cause parallel developments in various genetically unrelated plant groups, such as Bennettitales and angiosperms.

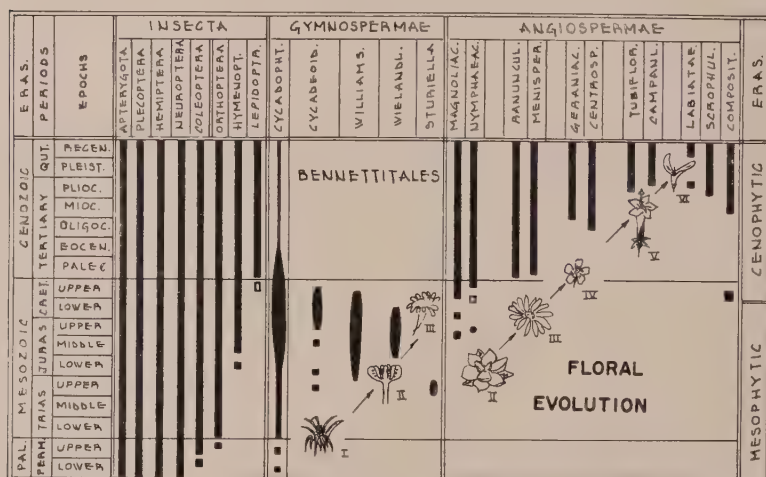


FIG. 8. Paleanthic evolution of the Bennettitales compared with the floral differentiation of angiosperms. Roman numerals indicate the evolutionary stages I-VI and corresponding type classes, as in table I. Notice the early occurrence of insects, long before the Bennettitales and Angiospermae. Differentiation of higher flower types (IV-VI) is correlated with the appearance and progression of Hymenoptera and Lepidoptera in the Cenozoic era.

The formation of certain flower types in unrelated plant groups by mediation of pollinating insects is clearly demonstrated by concrete examples among present-day flowering plants (33, 35, 41). It is of course a most embarrassing evolutionary process which may mold from almost any phylloid non-essential plant parts, such as bracts, upper leaves, involucre, functionless stamens, etc., most attractive imitations of flowers. The further development of such pseudanthia then is strictly obedient to the general sequence of floral evolution, as described above.

In the light of these facts the theory of recapitulation of flower types seems pertinent and applicable in the case of the Bennettitales

and angiosperms. The resemblance between the flowers of these two plant groups is so striking that most earlier students of paleobotany were tempted to derive angiosperms directly from the Bennettiales (57, 59, 66). No one, however, succeeded in these attempts, and the origin of angiosperms remained an inexplicable mystery, as it still is. To the present writer this resemblance seems to rest more upon the holetic homology of flower types, in a sense as described in a previous report (41, p. 469) rather than on the phylogenetic relationship of the Bennettiales and angiosperms. It is from this standpoint that the *paleomorphic* and *amorphic* types of the Bennettiales represent now the most desired and long sought intermediate stages, to supply the missing link in the general sequence of floral evolution.

The present theory of recapitulation of paleanthic flower types by early angiosperms provides a necessary precondition for a recent view of Scott *et al.* (60). These authors suggest a more shorter interval of geologic time between the origin of angiosperms and their first known appearance in the Cretaceous sediments, than is postulated commonly in the conventional theories.

As mentioned above, the amorphic stage, which so far has not been found among primitive angiosperms, has been assumed and described already in several former papers (32, 33, 40, 41). Haplo-morphic and actinomorphic types, on the contrary, are parallel developments, which occurred among lower angiosperms and higher Bennettiales at the same time, in the same Cretaceous strata. The parallel development of the Bennettiales and dicotyledonous angiosperms is confirmed now also by paleontological records. Axelrod (2) assumes that angiosperms occupied upland areas while Bennettiales lived in swamps. In the Albian deposits, however, the remains of *Magnolia*-like angiosperms are found side by side with the fossil remnants of Bennettiales (20). A recent finding of a fossilized leaf of the *Sassendorfites benkertii* by Kuhn from the lower Jura (Lias) is a new proof that the dicotyledonous angiosperms lived contemporaneously with Bennettiales (31, 46, 47).

The present study, consequently, supports neither the view of the genetic relationship between the Bennettiales and angiosperms, nor the attempt to derive the latter group from the first one. But it helps to co-ordinate the whole floral evolution into a continuous historical sequence, as follows: Amorphic→haplo-morphic→actinomorphic→pleomorphic→stereomorphic→zygomorphic (see fig. 8). This sequence has its beginning in the Triassic Bennettiales, and transmitted finally to the angiosperms, where its upper stages get their last touch. It is, of course, a long way from the Permian Cycadophyta up to modern angiosperms, a process which took at least 200 million years. It is a great advantage for the present study that the very early stages of this evolutionary sequence are adequately supplemented with paleontological findings in the Bennettiales and primitive angiosperms at the same time. This fact enables us to connect the whole sequence with paleontological records and to express the duration of this evolutionary cycle in terms of geological time table, as pictured in figure 8.

It seems reasonable to assume that Bennettiales were the only known group among gymnosperms, which have responded to the



selective challenge of insects with an outstanding evolutionary progress. They succeeded in developing showy flowers, but remained in their vegetative structure at the level of archaic Cycadophyta. Obviously their biochemic evolution did not progress fast enough and their primitive metabolism could not produce adequate amounts of concentrated sugars, proteins, colors, and odors to satisfy the increasing needs of insects. One can speculate that when the modern flowering plants appeared, Bennettitales had to give up their race, and since they were already too specialized in insect pollination, they could not return to wind pollination. Yet some anemophilous cycads, in spite of their primitive structure, survived to the present time.

Angiosperms, on the contrary, first taking over basic floral characteristics from the Bennettitales, showed an unusual genetic elasticity in their further evolution. Their phylogenetic youthfulness and modern body structure enable them to produce several new type classes and numerous special trends, adapted to increasing sensory abilities and selective activities of contemporary insects, birds, and bats. This must have accelerated the reciprocal development of modern plants and their pollinators.

#### SUMMARY

An attempt is made in this paper to co-ordinate the early flower types of Bennettitales, as far as they are established according to known paleontological records, to the evolutionary sequences of present-day flowering plants. It appears that the early evolution of the flowers of the Bennettitales is similar to the evolutionary sequence of angiosperms, and that the same type classes are represented in both plant groups. Beginning with amorphic flower types, which are represented only in the Bennettitales, the floral evolution is continued as a parallel trend in both plant groups, until the angiosperms, after the extinction of the first group, became the sole carriers of this evolutionary trend. To explain this phenomenon, a new theory of transmissibility of flower types from one plant group to another was elaborated, which proposes the mediation of pollinating insects in initiating and conducting certain parallel evolutionary trends in several plant groups.

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